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THE BEHAVIOR OF SOME SOIL INSECTS IN GRADIENTS OF EVAPORATING POWER OF AIR, CARBON DIOXIDE AND AMMONIA.¹

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I. INTRODUCTION.

The study of experimental ecology has started only within comparatively recent years and very little work has been done upon the relation of evaporation to the life economy of animals. The importance of the rate of evaporation as an environmental factor has been discussed by Shelford ('14a, b, c). Since evaporation is determined by the rate of air movement, humidity, temperature, pressure, and indirectly by illumination, it serves as an index of the general weather conditions. By varying any one of the factors controlling it, the rate of evaporation will be changed. The purpose of this paper is to show the behavior of some soil insects in evaporation, carbon dioxide, and ammonia gradients under experimental conditions.

II. METHOD OF STUDY AND MATERIAL.

1. *Method of Study.*

The method and equipment used in establishing the evaporation gradients was essentially the same as that described by

¹ Contribution from the Zoölogical Laboratory of the University of Illinois, No. 83.

Shelford and Deere ('13), except for the method of measuring and controlling the rate of air flow. This is new and will be described in some detail. The supply of air was secured from the University high pressure supply and was reduced from about 80 pounds to 5 pounds by a Mason reducing valve, which gave a constant pressure irrespective of the amount of air used. At room temperature, about 70° F., the air had a relative humidity of 18 to 20 per cent. The moisture was removed from the air by passing it through sulfuric acid filters, then through a glass-wool filter to remove any trace of the acid, a coiled aluminum pipe to regulate the temperature, and finally to the apparatus for controlling the rate of air flow. The sulfuric acid filters consisted of six chloride jars, 18 by 3 inches, filled with moderately fine pumice stone saturated with sulfuric acid. The medium moist air and saturated air was passed through glass-wool filters and then moistened by blowing it over or bubbling it through water in wash bottles. By passing the air into the bottles through glass tubes and regulating the height of the opening above the water almost any per cent. of saturation could be obtained. From the wash bottles the air passed through coiled aluminum tubes for regulating the temperature and then to the apparatus for regulating the rate of air flow.

The experimental cage for observing the behavior and modification of the insects, and the glass tubes for testing their resistance to evaporation and gases, were the same as those described by Shelford and Deere ('13). The experimental cage was 30 cm. long, 6.5 cm. wide, and 2.5 cm. deep. The glass tubes were each 21 cm. long and 3.2 cm. inside diameter. The lower third of each tube was filled with paraffin upon which sand had been sifted while it was still warm. From each of the tubes the air passed to a chamber containing a Livingston porous cup atomometer so that the evaporation could be recorded while the animals were being observed. For testing the relative humidity of the air two long chemical thermometers, graduated to 0.5 of a degree, were inserted with the bulb end inside a glass tube about 20 centimeters long and 2 centimeters in diameter, through which the air was allowed to flow. The wet bulb thermometer was provided with a wick which connected with a vial of distilled water.

Glass Y's were inserted in each air line between the aluminum coils and the apparatus for regulating the air flow. By means of these Y's, cross connections of the different air lines could be made or carbon dioxide could be introduced into the air. The carbon dioxide was obtained from a tank of compressed carbonic acid gas. The pressure was reduced and regulated by the use of a pressure reducing valve. The gas passed from the pressure gage through a rubber tubing to a two-way valve. By regulating the size of these openings different proportions of the gas could be passed into any two of the three air lines. The percentage of carbon dioxide in the air was determined by collecting the mixture in a burette over water and absorbing the carbon dioxide with a solution of sodium or potassium hydroxide in a Hemple pipette. Only a little work was done with ammonia and no method was used for determining the per cent. in the air. Different gradients of ammonia air were secured by bubbling the air in each of two lines through water bottles containing 1,000 c.c. of water to which had been added 30 c.c. and 60 c.c. respectively of a 1/10*N* solution of ammonia. Air from each of these lines turned moist litmus paper in a few seconds.

The apparatus for measuring and regulating the air flow, in the different thirds of the cage, is new and was designed by Professor V. E. Shelford and the writer. The principle involved is that of measuring, by means of an inclined manometer, the static pressure produced in a box or cylinder when the outlet is smaller than the inlet. The apparatus, Fig. 1, consists of three similar parts, one part for each third of the cage. The air enters the cylinders through the back, first, however, passing up to the top of the back-board where there is a screw-clamp for regulating the flow. Fig. 2 is a diagrammatic longitudinal section of the cylinder showing its connections with the inclined manometer. The cylinder is divided into two halves, each 3 inches long and 3 inches in diameter, which are constructed with a rim around the outside of the adjacent ends in such a way that they can be fastened together with thumbscrews. A thin circular diaphragm or disk, with a small hole in the center, is placed between the two adjacent ends and the connections are made air tight by a rubber gasket on each side. The opposite ends of the cylinder

have an inlet opening (*A*) and an outlet opening (*B*), each three eighths of an inch in diameter. On the upper side of each half of the cylinder are two openings (*E*) and (*F*) which are one fourth of an inch in diameter. These openings connect by rubber tubing to ends (*X*) and (*Y*) respectively of the inclined manometer.

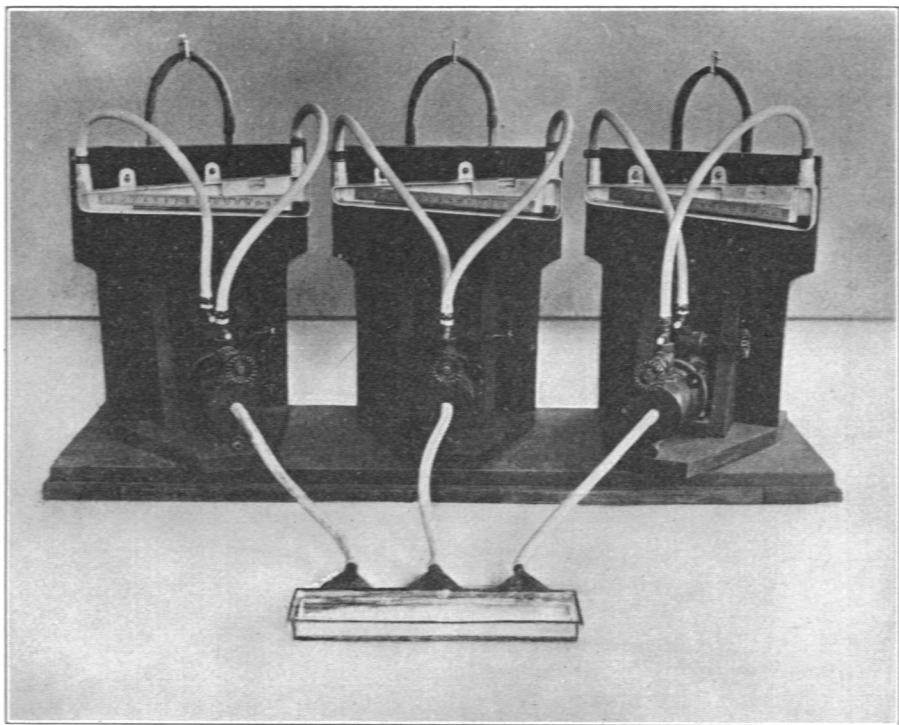


FIG. 1. Showing the three gages in position and connected with the gradient cage. The metal hood with symmetrical electric lights is removed. The valves make it possible to measure the pressure on either side of the diaphragm separately and thus check the results when both sides are connected.

The liquid used in the manometer was a red oil but the scale was corrected to read in millimeters of water. The amount of air entering chamber (1) through opening (*A*) is regulated by a screw-clamp (*T*) on the rubber tubing (*S*). The opening (*C*) in the diaphragm (*D*) should be in the center and may be any size smaller than openings (*A*) and (*B*). Since opening (*C*) is smaller than opening (*A*) the air cannot escape from the chamber

as readily as it enters and as a result static pressure is produced. This pressure is indicated through opening (*E*) on the inclined manometer. Further, since opening (*C*) is smaller than opening (*B*) the air escapes through (*C*) into chamber (2) the same as if into the free atmosphere or without exerting any static pressure. If, however, the rubber tubing connecting opening (*B*) with the

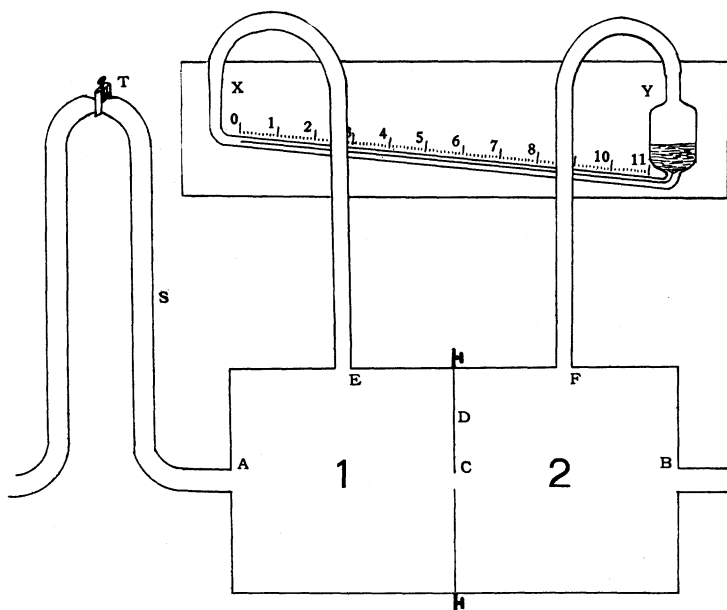


FIG. 2. Showing a diagrammatic section of the diaphragm chambers and gage. For description see text page 161. The number of units in the scale is here reduced to 11 for convenience. The number in the gages in use is 17, each representing one millimeter of water.

experimental cage is long or crooked, static pressure may be exerted in chamber (2) due to the friction of the air in the tubing, or the tubing may become kinked or closed in which case the air would pass out through opening (*E*) and the inclined manometer. To remedy this possible chance of error it is advisable to have chamber (2) connected with end (*Y*) of the manometer. If this is done only the difference in static pressure between chambers (1) and (2) is indicated or the actual amount of pressure exerted by the air flowing through opening (*C*). By using diaphragms with different-sized openings different volumes of air can be

measured. Openings almost as large as the inlet opening may be used for large flows of air and smaller openings for smaller flows of air.

The amount of air in pounds per second flowing through (C) may be determined by the following formula (Durley, '06); $.6299 CD^2 \sqrt{I/T}$, in which C is a constant approximately .602 for small openings and slight pressures, D is the diameter of the opening in the diaphragm in inches, I is the inches of water displaced, and T is the absolute temperature F . (absolute 0 is -459° F.). The constant C varies slightly for different-sized openings and different pressures, but this variation is so small, however, that it may be considered as negligible in computing the volume of air passing through each third of the experimental cage. The diameter of the opening in the diaphragms, for all of the experiments performed, was five sixteenths of an inch. The static pressure was recorded in millimeters instead of inches of water. By changing the millimeters to inches, substituting the necessary data in the formula and solving, the volume of air in pounds per second may be obtained. It was thought desirable, however, to give the volume in liters of air per minute. This may be obtained by multiplying the pounds per second by 60 to get the pounds per minute, then by 454 to get the grams per minute, and dividing by 1.1265, which is approximately the number of grams in one liter of air at 70° F. and a barometric pressure of 29 inches.

2. Material.

The material studied consisted of full grown larvæ and adults of the family Carabidæ. The following species of larvæ were used in the experiments: *Evarthrus sodalis* Lec., *Harpalus vagans* Lec., *Harpalus erythropus* Dej., *Pterostichus corvinus* Dej., and *Amara avida* Say. The species of adults studied were *Evarthrus sodalis* Lec., *Harpalus erythropus* Dej., *Harpalus pennsylvanicus* Dej., *Pterostichus corvinus* Dej., *Pterostichus stygicus* Say, *Amara avida* Say, *Anisodactylus nigrita* Dej., *Patrobus longicornis* Say, and *Patrobus placidus* Say. The material was collected at various times throughout the year and was kept in two-ounce tin boxes partly filled with moist soil. A few of the larvæ were

subjected to special treatment, which will be discussed under the experiments. The majority of the experiments on the larvæ were performed with the species *Evarthrus sodalis*. The larvæ of this species are about an inch long, vigorous, active, easily collected, and could be found in a variety of situations. They were dug in all kinds of situations, from dry or wet, black soil in corn fields to wet, sandy or humus soil close to creek beds. The larvæ of the genus *Harpalus* were mostly collected in wet, sandy soil close to a creek bed; but they were also taken in drier and heavier soil. The larvæ of the genus *Amara* were dug from wet, sandy soil close to a creek and from moist, black soil in the bottom of a depression which contained considerable humus. Larvæ of the genus *Pterostichus* were dug from situations similar to those of *Evarthrus sodalis*. The adults were collected at various places.

III. EXPERIMENTAL RESULTS.

About one hundred and twenty-five experiments were performed at various times during the fall, winter, and spring of 1915-16. Only a few representative ones, however, will be given and discussed, together with any peculiar variations which may need to be noted.

1. Larvæ.

A. Controls.—The controls, which were conducted in still air, were principally of two types as far as results were concerned. The larvæ were either active, crawling from one end of the cage to the other, but occasionally stopping at either end to try to crawl out, or they soon became quiet and remained in any part of it and appeared to rest or sleep. At temperatures of about 18° to 22° C. the larvæ were usually active and crawled from end to end of the experimental cage. At temperatures below 18° C. they were often inactive and remained quiet unless conditions were otherwise unfavorable. At temperatures of 23° C. and above the larvæ were sometimes inactive but not at ease. The increased temperature seemed to have a depressing effect and the larvæ acted tired and uneasy. Since in the normal controls the larvæ were either quite symmetrical in their movements or were quiet, it was not thought necessary to give the control for each experiment. Graph 1 shows the control for an *Evarthrus sodalis*

larva at a temperature of 20.5° C. The distance from the right to left represents the length of the cage and the vertical distance time. Graph 8 shows the control of another *Evarthrus sodalis* larva with a temperature of 23° C. at the start and 26.5° C. at the end.

B. Reaction in Evaporation and Temperature Gradients.—The experiments on evaporation were varied by changing the relative humidity, the temperature, and the rate of air flow. The flow of air used, unless otherwise stated, was 13.3 liters per minute. This volume of air was secured by using a diaphragm with an opening five sixteenths of an inch in diameter and a displacement of three millimeters of water.

Graph 2 shows the reaction of two *Evarthrus sodalis* larvæ to dry air at a temperature of 21° C. The avoidance of the dry air was very sharp and decided by one of them. The other larva rushed into the dry air, was soon overcome and was unable to get out. It squirmed and rolled about, became less active and was dead at the end of forty minutes. It had shrunk considerably, due to the withdrawal of water, and had turned a dirty yellow color. The larva which avoided the dry air was apparently as active at the end of the experiment as at the beginning. At lower temperatures the larvæ were generally not so active and did not avoid the dry air so sharply. Graph 3 shows the reaction of an *Evarthrus sodalis* larva to dry air at a temperature of 17° C. In the wet air it acted normal, except for some sluggishness. In the medium and dry air it squirmed and rolled about but was not affected as much as when the temperature was higher. Graph 4 shows the reaction of an *Evarthrus sodalis* larva, which had been outside in freezing weather for five days, to a high temperature and a low percentage of moisture. The behavior was different from those in dry air at lower temperatures in that the larva was sluggish, depressed and appeared fatigued. The effect appeared to be very similar to that of carbon dioxide, which will be described later. The graph shows the movement of the larva for forty minutes, the second twenty minutes starting at (X). At the end of the forty minutes the larva was considerably shrunk, was a creamy yellow color in the membranous areas, and appeared to be dead. It began to revive in a little over an

hour, but never fully recovered. Graph 5 shows the reaction of an *Evarthrus sodalis* larva, which had been outside in freezing and thawing weather for eighteen days, to dry air and a temperature of 22.5° C. There was a tendency in this larva to avoid the driest air. This is shown not so much by the time spent in the dry air but by the fact that in only one instance did the larva reach the end of the cage containing the dry air. It was in the dry air for a greater length of time than in the other air but this was due to its squirming, twisting and slower movements. Graph 6 shows the reaction of an *Evarthrus sodalis* larva, which had been outside in frozen ground for five days, to dry air at a temperature of 16.5° C. The larva was brought in from the outside and allowed to revive for a few minutes before the experiment was started. The larva behaved more normal than those in graphs 4 and 5 and showed a greater tendency to select air suitable to itself.

Graph 7 shows the reaction of an *Evarthrus sodalis* larva to different rates of air flow at a temperature of 18° C. and a relative humidity of about 44 per cent. Although the larva was affected by the different gradients of evaporation thus produced, it showed no tendency to select its air. The flow of air in the different thirds of the cage was 0, 13.3, and 69.5 liters, respectively, per minute. Graph 8 shows the control of an *Evarthrus sodalis* larva at a temperature of 23° C. at the start and 26.5° C. at the end. Graphs 9, 10, and 11 show the reactions of three *Evarthrus sodalis* larvæ to air of practically the same temperature and relative humidity in corresponding parts of the cage but with different rates of air flow for each experiment. In graph 9, with an air flow of 13.3 liters per minute or 3 millimeters of water displaced, the larva was affected by the dry air but showed little tendency to avoid it. In graph 10, with an air flow of 19.0 liters per minute or 6 millimeters of water displaced, the larva showed no tendency to avoid the dry air. It was, however, affected, and became sluggish and less active as the experiment continued. Graph 11 shows the reaction of an *Evarthrus sodalis* larva to an air flow of 22.4 liters per minute or a displacement of 9 millimeters of water. With this rate of air flow the larva selected the wet air and was in much better con-

CHART I.

Graph 1 shows the control of an *Evarthrus sodalis* larva in still air at a temperature of 20.5° C.¹

¹ Where different temperatures, relative humidities, rates of air flow, and percentages of gas are given, the one on the left side of the cage is named first, the middle second, and that on the right side last.

Graph 2 shows the reaction of two *Evarthrus sodalis* larvæ to dry air at a temperature of 21° C. Relative humidity of the air, wet 81 per cent., medium 47 per cent., dry 17 per cent. Rate of air flow 13.3 liters per minute. The larvæ had been kept inside at a temperature of 20 to 21 degrees C.

Graph 3 shows the reaction of an *Evarthrus sodalis* larva to dry air at a temperature of 17° C. Relative humidity of the air, wet 82 per cent., medium 55 per cent., dry 4 per cent. Rate of air flow 13.3 liters per minute. The larva had been kept inside at a temperature of 20° to 21° C.

Graph 4 shows the reaction of an *Evarthrus sodalis* larva, which had been kept outside in freezing weather for five days, to a high temperature and a low percentage of moisture. The experiment ran for forty minutes, the second half of the graph starting at "X." Temperature of the air, wet 28° C., medium 26.5° C., dry 25.5° C. Relative humidity of the air, wet 40 per cent., medium 26 per cent., dry 1 per cent. Rate of air flow 13.3 liters per minute.

Graph 5 shows the reaction of an *Evarthrus sodalis* larva, which had been kept outside in freezing and thawing weather for 18 days, to dry air and a temperature of 22.5° C. Relative humidity of air, wet 95 per cent., medium 63 per cent., dry 4 per cent. Rate of air flow 13.3 liters per minute.

Graph 6 shows the reaction of an *Evarthrus sodalis* larva, which had been outside in freezing weather for five days, to dry air and a temperature of 16.5° C. Relative humidity of the air, wet 94 per cent., medium 52 per cent., dry 4 per cent. Rate of air flow 13.3 liters per minute.

Graph 7 shows the reaction of an *Evarthrus sodalis* larva to different rates of air flow. Temperature 18° C. Relative humidity of air, 44 per cent. at the start and 39 per cent. at the end. Rates of air flow, 0, 13.3, and 69.5 liters per minute. Evaporation from atmometers for 20 minutes, 0, .94 c.c. and 2.25 c.c.

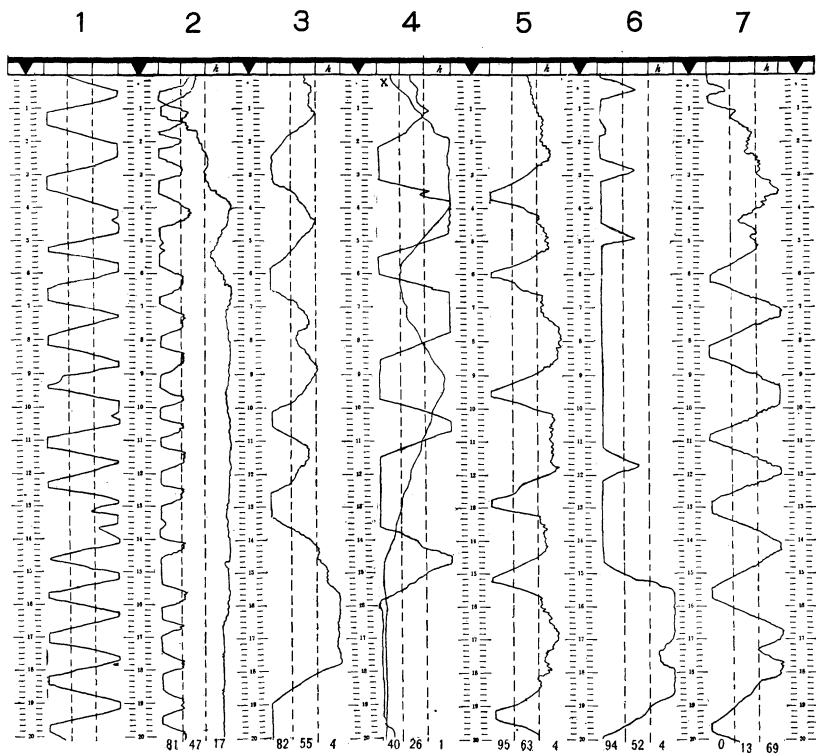


CHART II.

Graph 8 shows the control of an *Evarthrus sodalis* larva in still air at a temperature of 23° C. at the start and 26.5° C. at the end.

Graph 9 shows the reaction of an *Evarthrus sodalis* larva to an air flow of 13.3 liters per minute at a temperature of 22.5° C. Relative humidity of air, wet 54 per cent., medium 41 per cent., dry 7 per cent. Evaporation for 20 minutes, wet air .50 c.c., medium air .69 c.c., dry air 1.42 c.c.

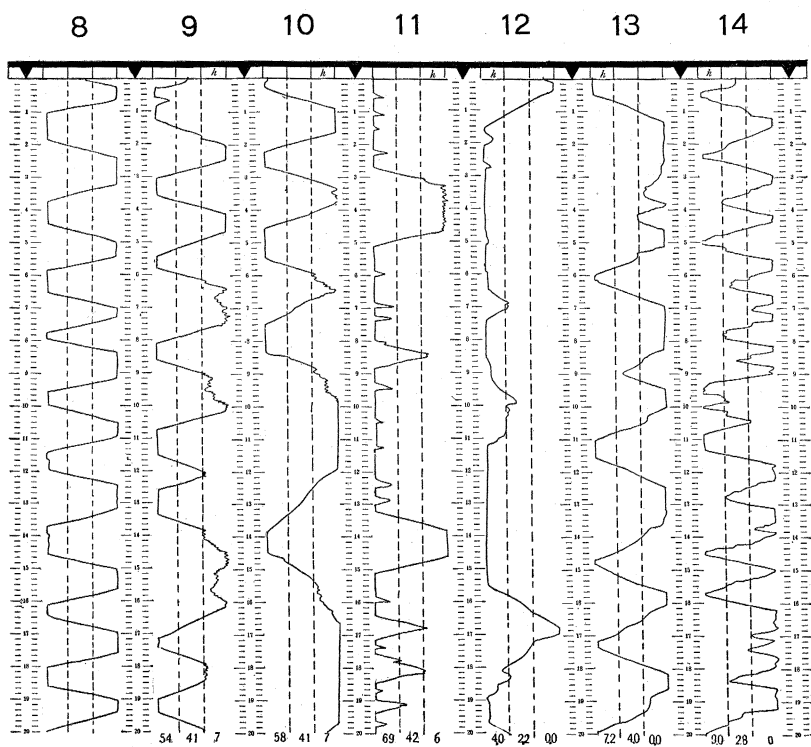
Graph 10 shows the reaction of an *Evarthrus sodalis* larva to an air flow of 19.0 liters per minute and a temperature of 22° C. Relative humidity of air, wet 58 per cent., medium 41 per cent., dry 7 per cent. Evaporation for 20 minutes, wet air .60 c.c., medium air 1.00 c.c., dry air 1.60 c.c.

Graph 11 shows the reaction of an *Evarthrus sodalis* larva to an air flow of 22.4 liters per minute and a temperature of 21.5° C. Relative humidity of air, wet 69 per cent., medium 42 per cent., dry 6 per cent. Evaporation for 20 minutes, wet air .54 c.c., medium air 1.07 c.c., dry air 1.75 c.c.

Graph 12 shows the reaction of an *Evarthrus sodalis* larva to a low percentage of carbon dioxide. Temperature 18° C. Relative humidity of air, 75 per cent. Rate of air flow 13.3 liters per minute. Per cent. of carbon dioxide in the different thirds of the cage, 4.0 (at left), 2.2, and 0.0.

Graph 13 shows the reaction of an *Evarthrus sodalis* larva to an increase in the per cent. of carbon dioxide. Temperature 18° C. Relative humidity of the air, 75 per cent. Rate of air flow 13.3 liters per minute. Per cent. of carbon dioxide in the different thirds of the cage, 7.2 (at left), 4.0, and 0.0.

Graph 14 shows the reaction of an unknown species of larva to a still higher percentage of carbon dioxide. Temperature 19° C. Relative humidity of the air, 95 per cent. Rate of air flow 13.3 liters per minute. Per cent. of carbon dioxide in the different thirds of the cage, 9.0 (at left), 2.8, and 0.0.



dition at the end of the experiment than either of the larvæ used in graphs 9 and 10.

In testing the resistance of larvæ to evaporation, in the glass tubes previously mentioned, one larva died at the end of 115 minutes' exposure in the tube containing the dry air at a temperature of 22.5° C. and a relative humidity of 9 per cent. The larvæ in the tubes containing the medium air, relative humidity 64 per cent. and temperature 22.5° C., and the wet air, relative humidity 95 per cent. and temperature 22.5° C., were not affected at the end of two hours. At a temperature of 23° to 24° C. another larva lived 75 minutes in the tube containing air with a relative humidity of 4 per cent., another one 120 minutes in the tube containing medium air with a relative humidity of 40 per cent., while in the tube containing the wet air, relative humidity about 80 per cent., the larva was slightly shrunk and inactive at the end of 160 minutes but not dead. The temperature had risen to about 26° C. when the experiment was discontinued. In testing the resistance of larvæ to gradients of evaporation, produced by different rates of air flow, at a temperature of 21.5° C. and a relative humidity of 7 per cent., one larva died after 35 minutes' exposure with an air flow of 16.4 liters per minute or 4.5 millimeters of water displaced. During this time 2.1 c.c. of water had evaporated from the porous cup atmometer. In air of the same temperature and relative humidity but an air flow of 13.3 liters per minute or 3 millimeters of water displaced, another larva died at the end of 68 minutes, with an evaporation of 3.2 c.c. of water from the porous cup atmometer. With an air flow of 9.3 liters per minute or 1.5 millimeters of water displaced a third larva died after 90 minutes' exposure with an evaporation for this period of 3.4 c.c. of water from the atmometer cup. The air was the same temperature and relative humidity as in the previous two experiments. The larva in the tube containing the larger flow of air was considerably disturbed from the first and rolled and twisted about. The larvæ in the other two tubes did not behave so violently but gradually became sluggish and less active until they died.

C. Reactions in Carbon Dioxide Gradients.—Graphs 12, 13 and 14 show the reaction of larvæ to air containing different percen-

tages of carbon dioxide at a temperature of 18° to 19° C. and a relative humidity of 75 to 95 per cent. In graph 12, with carbon dioxide percentages of 4.0, 2.2, and 0.0 respectively, an *Evarthrus sodalis* larva selected the air containing the largest amount of carbon dioxide. The larva used in graph 13, with carbon dioxide percentages of 7.2, 4.0, and 0.0 respectively, showed no marked preference for either the carbon-dioxide air or the carbon-dioxide-free air. In graph 14 an unknown species of larva showed a decided negative reaction to air containing 9.0 per cent. of carbon dioxide. No experiments were performed to determine the time of death of the larvæ in different amounts of carbon dioxide. In general, however, for mixtures of the gas up to 11 or 12 per cent. the larvæ were not violently affected. In air containing from about 7 to 12 per cent. of carbon dioxide they were sluggish and inactive and appeared fatigued. In percentages below this they sometimes selected the air containing the carbon dioxide and sometimes avoided it. They were not, however, much affected, if any, by low percentages of the gas. There was no violent squirming and twisting produced by the carbon dioxide but it seemed to have a depressing effect. The larvæ were sluggish, inactive, and appeared exhausted.

2. Adults.

A. Controls.—The behavior of the adults, both in the experiments and in the controls, was more irregular than that of the larvæ. They moved quicker and did not have the blind tendency to continue in the direction they were going if the conditions became unfavorable. Graph 15 shows two ten-minute controls for adults. The first ten minutes is the control for an *Evarthrus sodalis* adult and the last ten minutes the control for a *Patrobis longicornis* adult. Temperature 21° C. and no air flow. The *Evarthrus* adults showed a uniform tendency to run from one end of the cage to the other, while the majority of the other species often ran hesitatingly about for a time and then settled down and remained quiet, usually at one end of the cage.

B. Reactions in Evaporation and Temperature Gradients.—A number of experiments were performed with different species, but only a few can be given here. Graph 16 shows the reaction

CHART III.

Graph 15 shows the control for two species of adult Carabids. The first one half is the control for an *Evarthrus sodalis* adult and the second one half for a *Patrobis longicornis* adult. Temperature 21° C. No air flow.

Graph 16 shows the reaction of a *Pterostichus stygicus* adult to dry air and a temperature of 20.5° C. Relative humidity of air, wet 95 per cent., medium 86 per cent., dry 13 per cent. Rate of air flow 13.3 liters per minute.

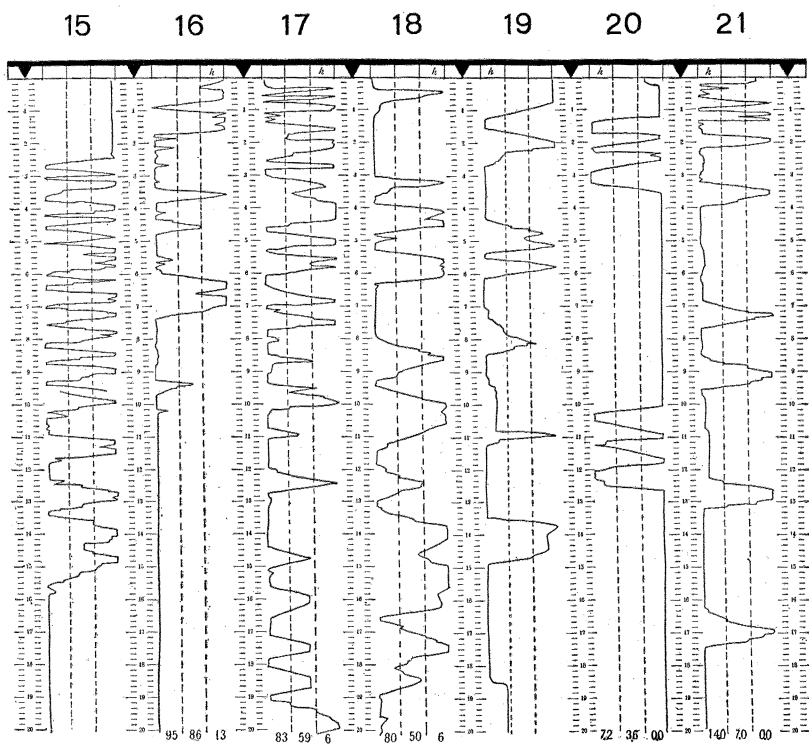
Graph 17 shows the reaction of a *Pterostichus corvinus* adult to dry air at a temperature of 19.5° C. Relative humidity of air, wet 83 per cent., medium 59 per cent., dry 6 per cent. Rate of air flow 13.3 liters per minute.

Graph 18 shows the reaction of a *Pterostichus corvinus* adult to dry air and a temperature of 16.5° C., with an increase in the rate of air flow to 19.0 liters per minute. Relative humidity of air, wet 80 per cent., medium 50 per cent., dry 6 per cent.

Graph 19 shows the reaction of an *Evarthrus sodalis* adult to gradients of ammonia. Temperature 22° C. Relative humidity of air, 98 per cent. Rate of air flow 13.3 liters per minute.

Graph 20 shows the reaction of a *Pterostichus stygicus* adult to gradients of carbon dioxide. Temperature 22° C. Relative humidity of the air, 90 per cent. Rate of air flow 13.3 liters per minute. Percentage of carbon dioxide in the different thirds of the cage, 7.2, 3.6, and 0.0.

Graph 21 shows the reaction of an *Evarthrus sodalis* adult to an increase in the percentage of carbon dioxide. Temperature 22.5° C. Relative humidity of the air, 86 per cent. Rate of air flow 13.3 liters per minute. Percentage of carbon dioxide in the different thirds of the cage, 14.0, 7.0, and 0.0.



of a *Pterostichus stygicus* adult to dry air at a temperature of 20.5° C. and an air flow of 13.3 liters per minute. The adult showed a tendency to move about at first but soon became inactive and remained quiet during the remainder of the experiment. It was active and in good condition when the experiment was discontinued. Graph 17 shows the reaction of a *Pterostichus corvinus* adult to dry air at a temperature of 19° C. and an air flow of 13.3 liters per minute. The adult did not show as decided a reaction against the dry air as the adult in the previous experiment but at the end of about eight minutes a preference was worked out for the wet air. Graph 18 shows the reaction of an adult of the same species to dry air at a still lower temperature, 16.5° C., and an increase in the rate of air flow to 19.0 liters per minute. Although the adult was restless and uneasy during the experiment, it showed little tendency to select the wet air.

To test the resistance of the adults to evaporation, three adults were put in the glass tubes with air flowing through them at a temperature of 21° C. at the beginning and 23° to 25° C. at the end, and a relative humidity at the end of 30 per cent. In the tube with an air flow of 13.3 liters per minute the adult died after 28 hours' exposure, during which time 70 c.c. of water had evaporated from the porous cup atmometer. In the tube with an air flow of 19.0 liters per minute the adult was dead at the end of 30 hours, during which time 77 c.c. of water had evaporated from the atmometer cup. In the third tube, with an air flow of 22.4 liters per minute the adult was dead at the end of 24 hours, during which time 82 c.c. of water had evaporated from the atmometer cup.

C. Reaction in Ammonia Gradients.—A few experiments were performed with air containing ammonia to determine the reaction of the adults to this gas. To obtain the gradients of ammonia in the air it was bubbled through water containing different amounts of the gas in solution. No quantitative determinations of the amount of ammonia in the air were made. Graph 19 shows the reaction of an *Evarthrus sodalis* adult to gradients of ammonia at a temperature of 22° C. and a relative humidity of 98 per cent. In this instance the avoiding reaction against the

ammonia was rather decided. The majority of the individuals tested showed considerable signs of disturbance and discomfort but they were not very strongly negative to ammonia; one or two continued to remain in the ammonia air although they were not at ease. The adults moved hesitatingly and at random in the ammonia air, stroking the antennæ and occasionally the abdomen.

D. Reaction to Carbon Dioxide.—The reaction of the adults to gradients of carbon dioxide was not very different from that of the larvæ. Graph 20 shows the reaction of an adult *Pterostichus stygicus* to air containing carbon dioxide gradients of 7.2, 3.6, and 0.0 per cent. with a temperature of 22° C. and a relative humidity of 90 per cent. The adult tried the carbon-dioxide-free air several times, but each time came to rest in the air containing the largest amount of the gas. Graph 21 shows the reaction of an adult of the same species to air containing carbon dioxide gradients of 14, 7, and 0.0 per cent. with a temperature of 22.5° C. and a relative humidity of 86 per cent. In this instance the adult showed a distinct negative reaction to the flow of air containing the largest per cent. of carbon dioxide, spending most of its time in the carbon-dioxide-free air. In most cases where the carbon dioxide was about 6 or 7 per cent., or higher, the adults either avoided it or were uneasy and distressed. With lower percentages of the gas very little signs of uneasiness were shown.

IV. SUMMARY AND DISCUSSION OF CONCLUSIONS.

A thorough understanding of the behavior of the soil insects to evaporation, temperature, and gases found in the soil necessitates a knowledge of the conditions existing in their habitat. This includes the physical condition of the soil, the temperature, the moisture, and the gases. The physical structure of the soil, *i. e.*, size of soil particles, porosity, amount of organic material, etc., is important, since it is upon these that the soil moisture, temperature, and aeration is dependent. The temperature of the soil is fairly constant. It does not have the range of variation and is not subjected to the sudden changes encountered in the atmosphere. This is more noticeably so in soil which is moderately moist to wet and is due, to a large extent, to the great

amount of heat used in the evaporation of water. Thus considerable heat can be used in the evaporation of moisture from wet or moist soil and the temperature of the soil itself will remain almost unchanged. On the other hand, in dry compact soil most of the heat is absorbed and the temperature of the soil is raised accordingly.

The moisture in the soil is derived largely from precipitation, but part of it may come from the adjacent soils or rock. The amount which a soil will retain is dependent upon the porosity, the physical structure, the litter covering the soil, and the growth of vegetation. A soil with a living vegetative cover loses moisture, both through direct evaporation and absorption by its vegetation, much faster than bare moist soil. The organic debris on the surface also conserves the moisture by the formation of a blanket or mulch. Evaporation is further retarded by the use of windbreaks or hindering the movement of the air over the soil, as has been shown by numerous experiments with windbreaks. Adams ('15) in discussing the soil moisture says: "McNutt and Fuller ('12) have made a study of soil moisture at 3 inches (7.5 cm.) and at 10 inches (25 cm.) below the surface in an oak-hickory forest, at Palos Park, Illinois. They found that the percentage of water to the dry weight of the soil at the 3-inch level averaged 18.9 per cent. and at 10 inches was 12.5 per cent. of the dry weight of the soil. The greater moisture near the surface is due to the humus present in this layer."

The ventilation and amount of air in the soil is dependent upon its physical properties, temperature and moisture. Dry soil, according to Hilgard ('06) contains from 35 to 50 per cent. its volume of air, and in moist or wet soil this space is replaced by water. Thus the conditions influencing the amount of water present have a very important influence upon aeration. The rapidity with which ventilation occurs is dependent upon the porosity and temperature; the greater the porosity and the higher the temperature, the more rapid the change. The amount of carbon dioxide in the soil is partly dependent upon the ventilation, the moisture, and the amount of decaying organic material. Since carbon dioxide is very soluble in water, it is found in the soil moisture in much larger proportions than in the atmosphere.

This concentration for different kinds of soil is shown by the following table by Bassungault and Lewy (Van Hise, '04).

Character of Soil Air.	CO ₂ in 10,000 Parts by Weight.
1. Sandy subsoil of forest.	38
2. Loamy subsoil of forest.	124
3. Surface soil of forest.	130
4. Surface soil of vineyard.	146
5. Pasture soil.	270
6. Rich in humus.	543

From this we see that the amount may reach as high as 5 or 6 per cent. in some situations.

Little is known concerning the occurrence of ammonia in soil air. It usually occurs in very small quantities but may occasionally be noticeable in places where there is much decaying organic matter. The small amounts of ammonia which may occur in the soil are usually held in electrolytic combination with the soil itself and do not occur free in the air.

The above is a very brief survey of some of the physical conditions which must be encountered by soil inhabiting insects. If we return to the experiments we will notice that the larvæ were very sensitive to evaporation, and especially so if the temperature was about 20° C. or above. This is what could be expected, since in their natural habitat the relative humidity of the air, in moist or wet soil, is not far below saturation and the temperature of the soil probably rarely goes above 20 to 23 degrees C., and then only in exposed, dry, hard soil in which one would not find the larvæ. It will also be noticed that of those larvæ which had been outside in freezing and thawing weather, the one experimented with at the lowest temperature behaved more normally and showed a greater tendency to select air probably suitable to its physiological condition. An increase in the rate of air flow, other conditions remaining the same, did not seem to affect the larvæ as much as an increase in temperature or a decrease in the relative humidity. They were probably affected more by the breathing in of the dry air and an increase in the temperature than by evaporation from the body surface. Their almost instantaneous detection of dry air and a high temperature would seem to point to this conclusion.

The increased temperature may have affected the larvæ by increasing their activity and metabolic processes, thus requiring a larger amount of air. If this air is dry, we can understand why the larvæ are more sensitive to dry air at the higher temperatures. On the other hand, if the temperature is lowered, their activity and metabolic processes are decreased, thus requiring a smaller amount of oxygen. In temperatures of 24° to 26° C. and above, the larvæ were often depressed, less active, and did not respond to the dry air so sharply. This may have been due to the fact that the temperature was increased above the point where their maximum activity occurred and that above this point an increased temperature had a depressing effect. In those experiments, in which the larvæ had been subjected to freezing weather for a number of days, the temperature at which the larvæ avoided the dry air the best was lowered from about 22° C. to 16° C. It was also noticed that larvæ collected early in the fall withstood high temperatures much better than those collected later.

The adults behaved somewhat similar to the larvæ in the experiments. They were more resistant to dry air and did not have the blind tendency to keep going ahead when the conditions became unfavorable. They often stopped and investigated the dry air, apparently sensing it with their antennæ. Their greater resistance to evaporation and temperature is natural, since they are usually found on the surface of the soil or near it, and are thus subjected to higher temperatures and drier air. Their increased chitinization of the body is also a greater protection from evaporation from the body surface.

The reaction of the larvæ and adults to carbon dioxide is not surprising when we consider their habitat and the amount of carbon dioxide found in the soil. No analyses of the moisture or the amount of carbon dioxide in the soil were made, but taking the figures available, the amount could not have been much below 4 per cent., which was selected by the larvæ in the experiments and which is probably their optimum. Insects are much more resistant to carbon dioxide than are warm-blooded animals and fishes (Shelford and Powers, '15) and can use practically all of the oxygen from a given quantity of air. This has been shown

by Shafer ('11) and other workers. Grasshoppers were left in pure carbon dioxide for 15 hours and adults of *Passalus cornutus* for 24 hours and complete recovery resulted. Large percentages of the carbon dioxide caused violent twisting and movements of the larvæ for a few minutes and then they became inactive and sluggish or stupefied. No experiments to determine their resistance to carbon dioxide were performed.

The experiments with the gradients of ammonia showed that the adults were affected by the gas but that they did not always react advantageously to it. The percentages used were probably considerably larger than that ever encountered in nature. Under some conditions of decaying vegetable matter considerable ammonia may, however, be present in the air.

In general the experiments show that the reactions of the larvæ and adults to gradients of evaporation, temperature, and carbon dioxide are similar to what one would expect from a study of their habitat. Adams ('15) in speaking of soil conditions says: "The animals which thrive in the soil are likely to be those which tolerate a large amount of carbon dioxide and are able to use a relatively small amount of oxygen, at least for considerable intervals, as when the soil is wet during prolonged rains. . . . The optimum soil habitat is therefore determined, to a very important degree, by the proper ratio or balance between the amount of available oxygen and the amount of carbon dioxide which can be endured without injury."

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